

A CONTRIBUTION TO THE TAXONOMY OF THE
ENCHYTRAEIDAE (OLIGOCHAETA). REVIEW
OF *STEPHENSONIELLA*, WITH NEW
SPECIES RECORDS

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Abstract.—The marine enchytraeid genus *Stephensoniella* Cernosvitov, 1934, (Oligochaeta: Annelida) is revised. Type-materials of four nominate species, *S. marina* (Moore, 1902), *S. barkudensis* (Stephenson, 1915), *Lumbricillus sterreri* Lasserre and Erséus, 1976, and *Marionina trevori* Coates, 1980, were examined. *Stephensoniella barkudensis* possesses a spermatheca with the same diverticulate ampullar structure as, and is a junior synonym of, *S. marina*, the type-species of the genus. *Lumbricillus sterreri* and *Marionina trevori* are transferred to *Stephensoniella* because they possess large, paired, unlobed seminal vesicles; nephridia with only the funnels in front of the septa; diverticulate spermathecal ampullae; thickened septa anteriorly; and only two or three setae in each setal bundle. *Stephensoniella* is structurally close to *Marionina* and *Lumbricillus*; however, a conservative evaluation of nephridial, spermathecal, and seminal vesicular characteristics distinguishes the species of each.

Stephensoniella was erected by Cernosvitov (1934) based on a redescription of the type-species, *Enchytraeus marinus* Moore, 1902. New material was collected from the type-locality, Gilson Hil Tip, Coney Sol, Bermuda, at the time of the redescription because the original material had been lost. Cernosvitov (1934) also transferred *Enchytraeus barkudensis* Stephenson, 1915 to *Stephensoniella* and these have remained the only recognized species. The major generic characters used by Cernosvitov (1934) to separate *Stephensoniella* from the closely related *Lumbricillus* and *Marionina* were the unlobed form of the seminal vesicles, the shape and distribution of the setae, and the diverticulate form of the spermathecal ampulla; and from *Enchytraeus*, the absence of peptonephridia and compact form of the penial bulb.

Nielsen and Christensen (1959) indicated that both species of *Stephensoniella* could be referred to *Marionina* but their unfamiliarity with the species caused them to refrain. They did point out, however, that *Marionina* is very heterogeneous, including several groups of species with only remote relations among them. Lasserre and Erséus (1976) echoed the view of Cernosvitov regarding the affinities of *Stephensoniella* and, although they could not clarify the genus definition, preferred to conserve it intact.

The examination of specimens of *S. marina* collected and identified by C. Erséus and the comparison of these with specimens of *Marionina trevori* Coates, 1980, revealed numerous structural similarities. Structural characteristics of *Lumbricillus sterreri* Lasserre and Erséus, 1976, brought to my attention by C. Erséus, led to the reexamination of that species and to the subsequent transferral of both these species to *Stephensoniella*.

I have attempted in the following systematic section to establish a homogeneous species grouping and to clarify those characteristics that distinguish *Stephensoniella*. All the described species that could be determined undoubtedly to belong in *Stephensoniella* have been included.

Materials

Type and additional material of the four species *Stephensoniella marina*, *S. barkudensis*, *Marionina trevori*, and *Lumbricillus sterreri* were borrowed from the British Museum (Natural History) (BMNH); the National Museum of Natural Sciences, Canada (NMCIC); the Muséum National d'Histoire Naturelle, Paris, France (AH); Smithsonian Institution, National Museum of Natural History (USNM); the personal collection of C. Erséus, Sweden (CE); and from EVS Consultants Ltd., Sidney, British Columbia (EVS). New, unmounted material was stained in alcoholic borax carmine, dehydrated through an ethanol to xylene series and mounted whole in Canada balsam.

Stephensoniella Cernovitov, 1934 (emended)

Type-species.—*Enchytraeus marinus* Moore, 1902.

Definition.—Brackish and littoral marine enchytraeids. Setae in 4 bundles from II; 2 or 3 setae per bundle in preclitellar segments, 2 (infrequently 3) in intra- and postclitellar segments; single-pointed, straight or slightly sigmoid, bent proximally. Head pore just anterior to 0/1, other dorsal, coelomic pores absent. Oesophageal-intestinal transition gradual, intra- or postclitellar. Peptonephridia, oesophageal and intestinal diverticula lacking, but with solid, paired, dorsal, post-pharyngeal bulbs. Pharyngeal glands well-developed, broadly united at 3/4, 4/5, and 5/6. Dorsal blood vessel origin intra- or postclitellar; dorsal vessel bifurcating anterior to brain, in prostomium. Lymphocytes nucleate. Chloragocytes present from preclitellar segments. Preseptal part of nephridia includes funnel only; interstitial tissue around postseptal nephridial canal well-developed; ectal duct terminal, ventral. Muscle layers of some of septa 6/7 to 9/10 thickened. Ovaries, testes and associated ducts and pores all paired, in typical familial positions. Seminal vesicles paired, unlobed. Sperm funnels (glandular vasa deferentia) well-developed; non-glandular vasa deferentia contained in XII, surrounded medially at ectal pores by compact penial bulbs, accessory prostatic glands absent. No ventral copulatory glands. Spermathecae paired in V, always attached to, if not actually communicating with, oesophagus via short ental ducts. Each ampulla with a rounded or ovoid diverticulum. Spermathecal ectal duct with or without glands.

Habitat and distribution.—Coastal marine, usually tropical or subtropical. Caribbean Sea; Atlantic Ocean—Bermuda, Florida, and Brazil; Indian Ocean—Barkuda Island, India; Persian Gulf—Saudi Arabia; northeast Pacific Ocean—British Columbia.

Remarks.—The primary distinguishing characteristics of the genus are the distribution of almost straight setae in bundles of only two or three; the thickened, muscular, preclitellar septa and well developed pharyngeal glands; the paired, unlobed seminal vesicles; and the single, rounded diverticulum found on each spermathecal ampulla. Rudimentary peptonephridia (see Stephenson 1915a), also

referred to in the literature as solid postpharyngeal bulbs and dorsolateral pharyngeal appendages, have been reported in species of *Marionina* (Kossmagk-Stephan 1983) and *Fridericia*, *Mesenchytraeus*, *Lumbricillus*, *Bryodrilus*, *Buchholzia*, and *Henlea* (Stephenson 1930) and are therefore not a good distinguishing characteristic.

Cernosvitov (1934) discussed the significance to the generic definition of *Stephensoniella* of the two-layered longitudinal epidermal musculature that he observed in *S. marina*. Stephenson (1930) had previously remarked that a two-layered longitudinal musculature occurred frequently in *Enchytraeus* and *Fridericia*. Later, Cernosvitov (1937) pointed out that two types of longitudinal muscle fibres (round and ribbon-like) were found in some species of *Achaeta*, *Guarani-drilus*, *Hemienchytraeus*, and *Fridericia*. These genera were not considered to be phylogenetically close and were placed (Cernosvitov 1937) in three different subfamilies. With only a limited amount of information about this musculature character and knowledge that the same arrangement occurs in phylogenetically dissimilar groups it is not possible to ascertain the taxonomic significance of the characteristic.

The species of *Stephensoniella* can be distinguished from each other by their different absolute sizes and by the distribution of gland cells around the spermathecal ectal ducts.

Stephensoniella marina (Moore, 1902) (emended)

Figs. 1-3

Enchytraeus marinus Moore, 1902:80-82.

Stephensoniella marina (Moore).—Cernosvitov, 1934:233-237, 242-243; Cernosvitov, 1935:8.

Stephensoniella marina (Moore).—Lasserre and Erséus, 1976:455.

Enchytraeus barkudensis Stephenson, 1915b:142.—Stephenson 1915a:45-47; 1923:113-114.

Stephensoniella barkudensis (Stephenson)—Cernosvitov, 1934:242-243.

Stephensoniella barcudensis (Stephenson)—Cernosvitov, 1937:291.

Material examined.—BMNH 1949.3.1.1010, whole mount (originally labelled by Cernosvitov as *Enchytraeus neotropicus* n. sp. [a name which was never subsequently published], Mus. Paris #3764), BMNH 1949.3.1.1011, 3 slides of a transversely sectioned specimen, one slide of a longitudinally sectioned specimen, French Guyana (see Cernosvitov 1935); BMNH 1949.3.1.1012-1014, 4 whole mounts, 3 slides, immature, BMNH 1949.3.1.1015, 3 slides of a longitudinally sectioned specimen, collected by J. A. G. Wheeler, Gilson Hil Tip, Coney Sol, Bermudas, 8 Feb 1933 (see Cernosvitov 1934); CE 22H, 2 whole mounts, partially mature, collected by P. Lasserre, Coney Island, Bermuda, 1973 (see Lasserre and Erséus 1976); CE M77-1, one slide of a longitudinally sectioned specimen, CE M77-2, one whole mount and 2 mounted, partly dissected specimens, 2 slides, collected by C. Erséus, Virginia Key, Florida, 15 Nov 1977; and EVS, 17 whole mounted specimens, collected by Saudi Arabian Tetra Tech Inc., Persian Gulf, Saudi Arabia, 1981-1982.

As *S. barkudensis*: BMNH 1933.5.25.348, one slide of a longitudinally sectioned specimen, and BMNH 1933.5.25.351, one slide of a longitudinally sectioned specimen.

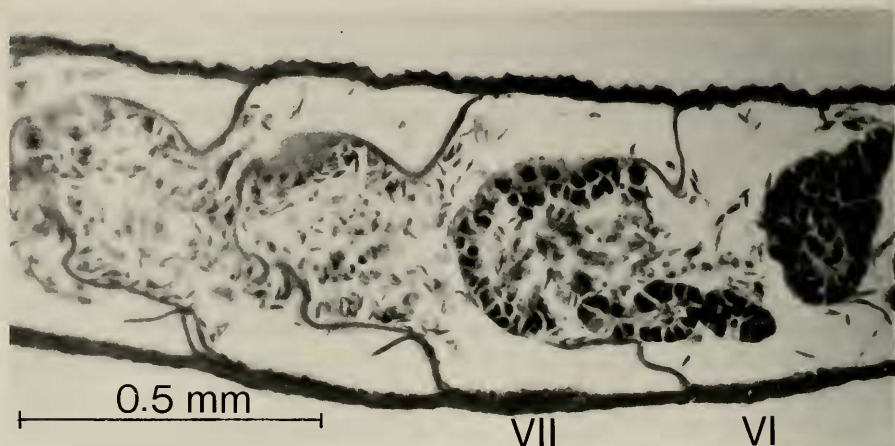


Fig. 1. *Stephensoniella marina*, section through anterior segments showing posteriorly distended, thickened septa 6/7, 7/8 and 8/9 (from *Enchytraeus barkudensis*, BMNH 1933.5.25.348).

tioned specimen, syntypes, Chilka Lake, Barkuda Island, India, collected 1914 (see Stephenson 1915b); BMNH 1933.5.25.355–357, 3 slides, 2 longitudinally sectioned specimens, Ennur, Madras, India (see Stephenson 1915a).

Description.—Length 6 to 10 mm, 46 to 73 segments; diameter to 0.5 mm. Cutaneous glands in 3 or 4 transverse rows per segment. Clitellum over XII and XIII, glands in numerous, regular transverse rows. Setae straight, 33, 50 to 120, usually 80 to 90 μm long; setae of II markedly short, 50 to 60 μm ; lateral setae shorter than ventrals of same segment. Two or 3 setae in anterolateral bundles, 3 setae in ventral bundles to X or XI, 2 (occasionally 3) setae in postclitellar segments. Septa (rarely 6/7) 7/8 to 9/10 thickened (Fig. 1). Lymphocytes abundant anteriorly, 20 to 30 μm long. Dorsal blood vessel origin postclitellar, to XXIII. Postclitellar segments with intra-segmental muscular bands extending from the circular epidermal muscles to muscles of gut. Seminal vesicles extending to 9/10; eggs confined to clitellar segments. Sperm funnels 2 to 3 times as long as wide, length just less than body width; glands differentially developed around ciliated duct; collar 2 or more times as wide as glandular part. Vas deferens 14 to 24 μm wide, non-muscular. Penial bulbs (Fig. 2A) 53 to 68 μm high, medial to vasa deferentia. Male pore simple. Spermathecal pores at 4/5, just ventral to level of lateral setae. Ectal ducts of spermathecae 14 to 26 μm wide, 3 to 4 times as long as wide; aglandular; communicating basally with ampulla at constriction between ampulla and thinner walled, dorsally directed diverticulum. Ampulla approximately 50 μm wide \times 80 μm long, diverticulum approximately 30 μm wide \times 90 μm long, more or less ovoid (Fig. 2B–D). Ampullae connecting laterally to oesophagus in posterior of V. Sperm densely bundled in diverticula, in random masses in ampullae.

Habitat.—Estuarine salt lakes and littoral and supralittoral marine, usually in medium coarse sands. With *Pontodrilus bermudensis*, in India (Stephenson 1915b).

Distribution.—Barkuda Island, India; French Guyana; Florida, U.S.A.; Bermuda; Persian Gulf, Saudi Arabia.

Remarks.—Examination of syntypes of *S. barkudensis*, BMNH 1933.5.25.348 and .351, and other specimens from Ennur, Madras, and Cernosvitov's material of *S. marina* revealed a few misinterpretations in, and omissions from, the literature. It was found that the spermathecal ampullae of *S. barkudensis* (Fig. 2D) each bore a basal, ovoid diverticulum as in *S. marina* (Fig. 2B, C). It is recorded at the British Museum (personal communication, E. G. Easton) that their material of *S. barkudensis* originated from the Indian Museum; it was simply labelled "types" when received and it is doubtful that a designated holotype remains in the Indian Museum.

Other than a broad geographical separation, partially bridged by the new records from the Persian Gulf, reasons supporting a classificatory distinction of *S. barkudensis* from *S. marina* are not found (Fig. 3). By seniority, *S. marina* (Moore, 1902) has precedence for the specific name; by original designation (Cernosvitov 1934), it is the type-species of the genus.

Stephensoniella sterreri (Lasserre and Erséus, 1976), new combination
Fig. 3

Lumbricillus sterreri Lasserre and Erséus, 1976:453–454 (partim).

Material examined.—Holotype: AH 193, a whole mount, Ireland Island, Bermuda, collected by P. Lasserre, 1973. Paratypes: AH 195, 196, 2 whole mounts, Coot Pond, Bermuda, collected by P. Lasserre, 1973.

Description.—Holotype with 47 segments, paratypes with 41 and 39 segments. Setae 3 per bundle in at least some preclitellar ventral bundles, 2 in other bundles, slightly sigmoid, 50 to 60 μm long. Clitellum incomplete ventromedially, between male pores. Some of septa 7/8 to 9/10 thickened. Vasa deferentia approximately 13 μm wide, opening ectally via simple pore, lateral to small penial bulb. Seminal vesicles and testes unlobed. Spermathecal ectal duct relatively short, 33 to 43 μm long, bulbous near middle, 17 to 26 μm wide. Glandular cells originating along length of duct, rosette of larger glands originating around ectal pore (Fig. 3). Spermathecal ampulla ovoid, approximately 51 to 61 μm wide and 86 to 91 μm long, approximately 1.5 times as long as wide. Subapical diverticulum nearly globular, 51 to 54 μm in diameter.

Remarks.—Characteristics not given in the description are as originally described (Lasserre and Erséus 1976) or as for the genus. The primary characteristics distinguishing *S. sterreri* from the type species (Fig. 3) are its small size and its spermathecal structure including the position of the origin of the diverticulum, relative shapes and sizes of the ampulla and diverticulum, and the presence of glandular cells on the ectal duct. Three setae may be present in very few anteroventral setal bundles, as in paratype AH 196 with three setae only in X and XI.

The Muséum National d'Histoire Naturelle in Paris had no deposition records for paratype AH 197 (J. Renaud-Mornant, personal communication) (see Lasserre and Erséus 1976). Paratype AH 194 has been referred to *S. trevori* (see page 416).

Habitat.—Mid-littoral in medium or coarse sands rich with organic debris.

Distribution.—Bermuda.

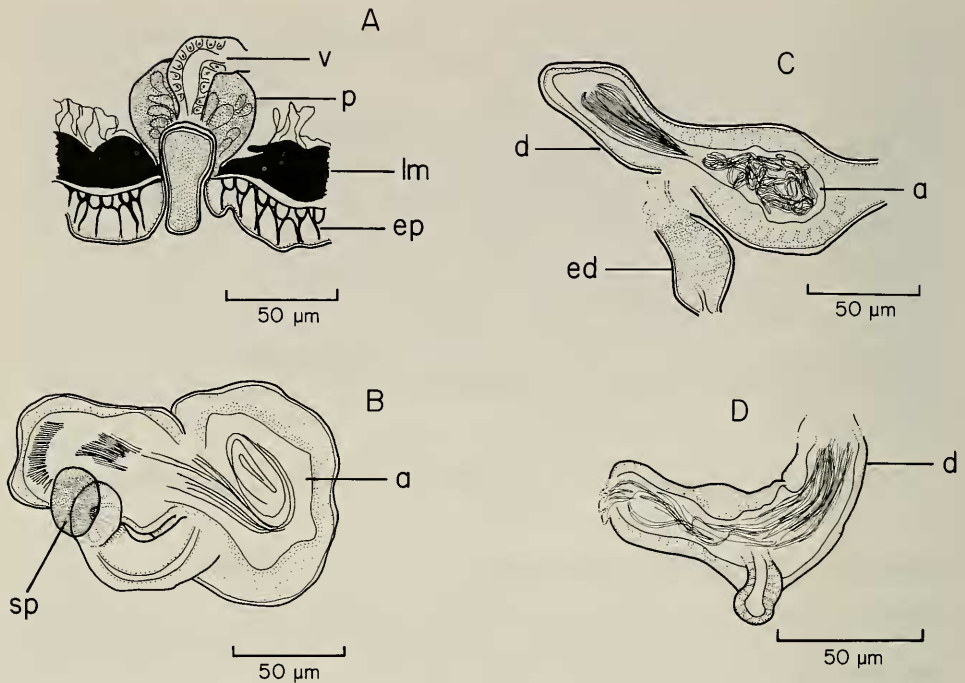


Fig. 2. *Stephensoniella marina*. A, Longitudinal section of glandular penial bulb (p) in XII, vas deferens (v) opens into a narrow epidermal invagination (from CE M77-1, Virginia Key, Florida); B, Lateral view of spermatheca in V, foreshortened, whole mounted specimen (from CE M77-2, Virginia Key, Florida); C, Sectioned spermatheca in V (from CE M77-1); D, Sectioned spermatheca showing distinct ampulla and diverticulum, with ectal duct communicating with the ampulla at the origin of the diverticulum (from *Euchytraeus barkudensis*, BMNH 1933.5.25.356, Madras, India). Other abbreviations: a, spermathecal ampulla; d, ampullar diverticulum, extending dorsad; ed, ectal duct; ep, circular muscle (black) and epithelial cell layer covered by cuticle; lm, longitudinal muscle; sp, ectal spermathecal pore.

Stephensoniella trevori (Coates, 1980), new combination

Fig. 3

Marionina trevori Coates, 1980:1311–1313.—Coates and Ellis, 1981:2137.

Lumbricillus sterreri Lasserre and Erséus, 1976:453–454 (partim).

Material examined.—Holotype: NMCIC 1979-1599, whole mount, Qualicum Beach, British Columbia, Canada, collected by K.A. Coates, 10 June 1976. Paratypes: NMCIC 1979-1600; and USNM 58913, whole mounts, Qualicum Beach, British Columbia, Canada, collected by K. A. Coates, 10 June 1976. Other material: AH 194, a paratype of *Lumbricillus sterreri*, whole mount, Shelly Bay, Bermuda, collected by P. Lasserre, 1973; CE, 10 whole mounted specimens, just north of Cabo Frio, coast of Brazil, collected by J. Renaud-Mornant, 15 Oct. 1976; and EVS, 56 whole mounted specimens, Persian Gulf, Saudi Arabia, collected by Saudi Arabian Tetra Tech Inc., 1981–1982.

Description.—Setae slightly sigmoid, to 74 μ m long; infrequently with 3 setae in postclitellar bundles. Clitellum incomplete medioventrally between male pores. Septa 8/9 and 9/10 thickened. Seminal vesicle extending as far anterior as pos-







	<i>marina</i> (Moore)		<i>sterreri</i>	<i>trevori</i>
	as <i>marina</i>	as <i>barkudensis</i>	(Lasserre & Erseus)	(Coates)
no. of segments	55-73	46-48, 64-67	39-47	35-50
dorsal vessel origin	XIV-XXIII	XII-XXII	XII-XIII	XII-XIII
sperm funnel L:D	2-3:1	2-3:1	2-4:1	2:1
sperm funnel collar	wide		equal funnel	equal funnel
thickened septa	(6/7) 7/8-9/10	7/8-9/10	7/8-9/10	8/9-9/10
setae				
spermathecae				

Fig. 3. Distinguishing characteristics of three species of *Stephensiella*. Scale bar equals 50 μ m. Figure of spermatheca of *S. sterreri* modified after Lasserre and Erséus (1976: fig. 3C).

terior thickened septum. Vas deferens 10 to 14 μ m wide, regular throughout length, 2 to 3 times as long as sperm funnel; exiting via simple pore lateral to small penial bulb. Spermathecal ampulla and subapical diverticulum approximately globular, both 41 to 65 μ m in diameter; spermathecal ectal duct long and uniformly narrow, 11 to 17 μ m wide by 36 to 56 μ m long; with glands originating only around ectal pore.

Remarks.—Other characteristics are as described for the genus or as previously described (Coates 1980; Coates and Ellis 1981). *Stephensiella trevori* is distinguished from *S. marina* (Fig. 3) by size and spermathecal characteristics, as discussed for *S. sterreri*. It is distinguished from the latter species by the distribution of gland cells only around the pore of the ectal duct of the spermatheca and by the relative dimensions of the duct, ampulla and diverticulum of the spermatheca (Fig. 3).

Spermathecal characteristics have been relied upon quite heavily to distinguish the two smaller species of *Stephensiella*; however, the uniformity of spermathecal structure observed between and within widely separated populations of both *S. marina* and *S. trevori* provides a good basis for this reliance.

The whole mounted specimen of *S. trevori* from Bermuda (paratype AH 194 of *Lumbricillus sterreri*) illustrated by Lasserre and Erséus (1976: Plate 1B) is 0.2 mm wide, not 0.5 mm as would be determined from the illustration. The extension posteriad of the seminal vesicles previously noted (Coates 1980) may be an ar-

tefact of fixation or simply related to the volume of the seminal vesicles which do not extend anterior to the most posterior thickened septum.

Habitat.—Upper or mid-intertidal in sand with organic debris and finer sediments.

Distribution.—Qualicum Beach, British Columbia, Canada; Shelly Bay, Bermuda; Persian Gulf, Saudi Arabia; and Brazil.

Discussion

When *Stephensoniella* was first diagnosed (Cernosvitov 1934) it was recognized as phylogenetically close to *Lumbricillus* and *Marionina*. More recently (Nielsen and Christensen 1959) the structural diversity in *Marionina* has been allowed broader limits and the species of *Stephensoniella* could be included in that genus. *Stephensoniella*, however, combines at least two character states that are uncommon in *Marionina*, a nephridium with only the funnel anterior to the septum and paired, voluminous seminal vesicles. Distinct, large spermathecal diverticula, seen in all of *S. marina*, *S. trevori*, and *S. sterreri*, are unknown in both *Marionina* and *Lumbricillus*. Thickened, muscular, preclitellar septa are also distinctive for the three *Stephensoniella* species. It would not be surprising if other species presently classified, with reservations, as *Marionina* or *Lumbricillus* were found to belong in *Stephensoniella*.

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